

NEW SPECIES AND COMBINATIONS IN *SOLANUM*
SECTION *ANDROCERAS* (SOLANACEAE)

Stephen R. Stern

Department of Biological Sciences
Colorado Mesa University
1260 Kennedy Ave
Grand Junction, Colorado 81501, U.S.A.
ssstern@coloradomesa.edu

Lynn Bohs

Department of Biology
University of Utah
257 South 1400 East
Salt Lake City, Utah 84112, U.S.A.

Jeffrey Keeling

Department of Biology
Sul Ross State University
Alpine, Texas 79832, U.S.A.

ABSTRACT

A new species of *Solanum* from Texas is described here. *Solanum cordicitum* S. Stern is a member of *Solanum* section *Androceras*. It is similar to *S. citrullifolium* and *S. davisense* but differs from both in having white corollas, and differs from the latter in having inflorescences with a significantly longer axis and larger flowers. In addition to the new species, three new combinations are proposed for species in *Solanum* section *Androceras*, *Solanum setigeroides* (Whalen) S. Stern, *Solanum novomexicanum* (Bartlett) S. Stern, and *Solanum knoblochii* (Whalen) S. Stern.

RESUMEN

Se describe aquí una especie nueva de *Solanum* de Texas. *Solanum cordicitum* S. Stern es un miembro de *Solanum* sección *Androceras*. Esta especie es similar a *S. citrullifolium* y *S. davisense*, pero se diferencia de ambas por tener flores con corola blanca, y de la última por sus inflorescencias más largas y flores más grandes. También se proponen tres combinaciones nuevas de *Solanum* sección *Androceras*, *Solanum setigeroides* (Whalen) S. Stern, *Solanum novomexicanum* (Bartlett) S. Stern, y *Solanum knoblochii* (Whalen) S. Stern.

INTRODUCTION

A comprehensive project to complete species-level taxonomic treatments and resolve phylogenetic relationships within the genus *Solanum* L., supported by the National Science Foundation Planetary Biodiversity Inventory program, has facilitated detailed systematic study of many little known groups within this giant genus (Knapp et al. 2004; <http://www.nhm.ac.uk/solanaceaesource>). One of the largest groups within *Solanum*, the *Leptostemonum* clade, includes approximately 350–400 species (Bohs 2005; Levin et al. 2006; Weese & Bohs 2007; Stern et al. 2011) and is commonly known as the “spiny solanums” due to the presence of prickles. Phylogenetic work on this clade has identified a number of monophyletic groups, one of which corresponds to *Solanum* section *Androceras* (Nutt.) Whalen (Stern et al. 2010).

Solanum section *Androceras* is an unusual group within the spiny solanums due to its floral characteristics, namely its bilaterally symmetrical, heterantherous, and enantiostylous flowers. Most *Solanum* species have fleshy berry fruits, but those of section *Androceras* are dry with a prickly, accrescent calyx. The section has flavonoids that are unique among known flavonoids in other *Solanum* groups and has an atypical north temperate geographic distribution. Whalen (1979) provided a detailed revision of the section and included 12 species and 10 varieties. Stern et al. (2010) used molecular phylogenetic techniques to examine the relationships among these taxa. Results from that study, and further taxonomic work on *Solanum* section *Androceras*, have uncovered an undescribed *Solanum* species from Texas and indicates that some taxa described as varieties should be recognized as distinct species. These new names and combinations are validated here. A revision of Whalen's (1979) species key, including the 16 currently recognized species, is also provided.

Solanum cordicitum S. Stern, sp. nov. (Figs. 1–2). TYPE: UNITED STATES. TEXAS, Jeff Davis Co.: Valentine, Blk 76, Bell 2nd Add., 23 Sep 1990 (fl, fr) H. Elder 46 (HOLOTYPE: TEX [00402851]).

Similar to *Solanum citrullifolium* and *S. davisense*; differs from both in having white corollas; differs from *S. davisense* in having inflorescences with a significantly longer axis and larger flowers.

Herb to 35 cm. Stems armed with acicular prickles to 5 mm in length, tan to brown, the base to 1 × 0.5 mm, sparsely pubescent with simple, uniseriate, multicellular hairs 1–2 mm long, moderately pubescent with simple, uniseriate, multicellular, gland-tipped hairs 0.5–1 mm long. Flowering portions of stem of difoliate sympodial units, the leaves usually geminate, those of a pair often slightly unequal. Leaves simple, the blades 3–8 × 1.5–4 cm, deeply lobed to pinnatifid or pinnatisect with 3–4 lobes per side, chartaceous, green on both surfaces, the adaxial surface nearly glabrous with occasional simple, uniseriate, unicellular to multicellular hairs 0.5–1 mm long, the abaxial surface sparsely pubescent with stellate hairs, the stalks absent to 0.5 mm, multiseriate, the rays 2–4, 0.5–1 mm long, unicellular to multicellular, the midpoints 0.5–1 mm long; venation pinnate, the secondary veins 3–4 on each side of the midvein and one per lobe, the midrib and larger secondary veins occasionally with a few prickles like those of the stem; base obtuse, often asymmetrical; margin deeply lobed and the lobes with irregularly undulate margins; apex rounded to obtuse; petioles 0.5–3 cm, moderately pubescent with hairs like those of the stem, sparsely armed with prickles like those of the stem. Inflorescence 8–12 cm, extra-axillary, unbranched, with 5–8 flowers, the axes moderately pubescent with hairs like those of the stem, moderately armed with prickles like those of the stem; peduncle 2–3 cm; rachis 6–12 mm; pedicels 4–10 mm in flower, 10–18 mm in fruit, spaced 6–12 mm apart, articulated at the base. Flowers 5-merous, zygomorphic, enantiostylous. Calyx 4–6 mm long, the tube 1.5–3 mm, the lobes 2–4 × 0.5–1.2 mm, narrowly triangular, moderately pubescent abaxially with hairs like those of the stem, moderately armed with prickles like those of the stem; fruiting calyx 9–13 mm, strongly accrescent, completely covering the fruit, densely armed with prickles like those of the stem. Corolla 2–2.5 cm in diameter, chartaceous, white, rotate-stellate, with abundant interpetalar tissue, shallowly lobed, the lobes 2–3 × 0.5–1.5 mm, narrowly triangular, sparsely pubescent on abaxial midveins with hairs like those of the stem, adaxially glabrous. Stamens dimorphic, the lowermost one 10–12 mm, the upper four 5–8 mm; filaments 1–2 mm long, glabrous; lowermost anthers 9–11 × 1–2 mm, opposite the style in alternating right and left-handed flowers, distally curved upward, yellow; upper anthers 5–6 × 1–2 mm, straight, yellow, all anthers linear-lanceolate, tapering, the base cordate, the apex acute, the pores directed slightly introrsely, not opening into longitudinal slits. Ovary glabrous; style 10–14 × 0.5–1 mm, cylindrical, glabrous, opposite the lowermost anther and alternating between right and left-handed flowers; stigma to 1 mm wide. Fruit 10–12 mm in diameter, globose, tightly invested in the prickly accrescent calyx creating a burr-like fruit, green, turning black, drying and tearing apart at maturity, glabrous. Seeds 30–40 per fruit, ca. 1.5 × 1 mm, chocolate-brown, reniform, the surface with raised ridges.

Distribution and Phenology.—Known only from Jeff Davis Co., Texas from 1350–1820 m in elevation. The specimens were flowering in September–November and fruiting in September–November.

Etymology.—*Solanum cordicitum* is taken from the Latin “cordicitus“ for “from the heart” referring to the type locality of Valentine, Texas.

Conservation Status.—The conservation status of *S. cordicitum*, according to the IUCN Red List Categories (IUCN 2010) is Data Deficient due to the low number of collections. Despite searching herbaria, including BRIT, NY, TAES, TAMU, TEX, US, and UTEP, and collection efforts near Valentine, Texas in 2010 and 2013, only three collections of *S. cordicitum* are known. It is our hope that this species description will encourage further collecting in Jeff Davis County so that the status of *S. cordicitum* can be determined.

Solanum cordicitum has an overlapping geographic distribution with various members of section *Androceras*, including *S. rostratum*, *S. davisense*, both varieties of *S. tenuipes*, and *S. citrullifolium* vars. *citrullifolium* and *setigerum*. Unlike any of these species, *S. cordicitum* has white corollas. Additionally, *S. cordicitum* differs from *S. rostratum* in that the latter has stellate hairs on the stem while those of *S. cordicitum* are simple. *Solanum tenuipes* is typically found further south in the Big Bend area of Texas and is a perennial whereas *S. cordicitum* is an annual. The leaves of *S. cordicitum* are not thrice pinnatifid as they are in *S. davisense* and the lowermost

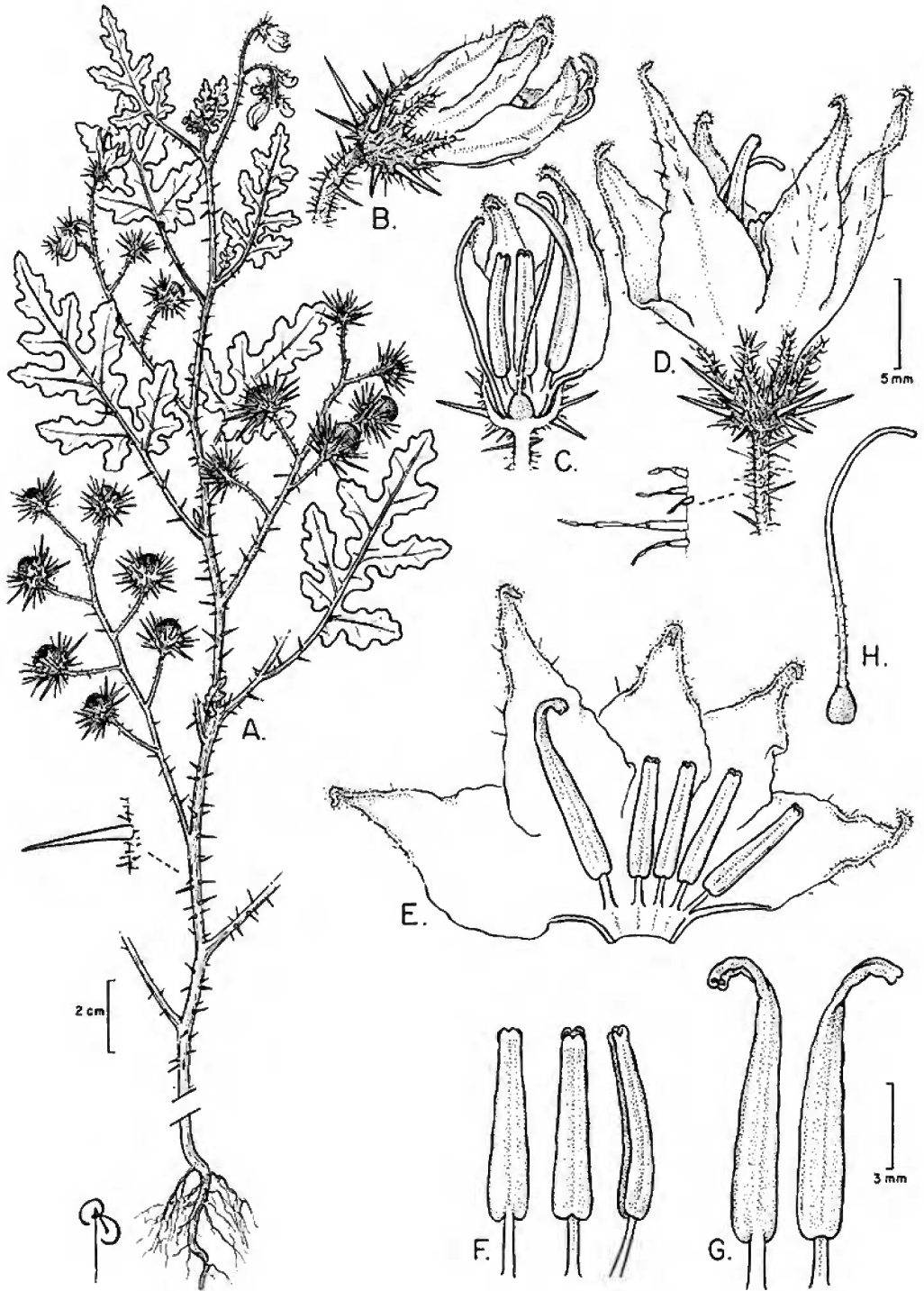


FIG. 1. *Solanum cordicum* S. Stern. A. Habit. Note zygomorphic flower buds. B, C, D. Flowers. E. Dissected corolla. Note elongate lower anther. F. Upper stamens. G. Lower stamen from a left- and right-handed flower. All from *H. Elder 46* (TEX).



Fig. 2. Holotype of *Solanum cordicum* S. Stern [Elder 46 (TEX)].

anthers of the latter are shorter (6–8 mm in *S. davisense* versus 9–11 mm in *S. cordicitum*). *Solanum cordicitum* also has longer inflorescences than *S. davisense* (8–12 cm in *S. cordicitum* versus 4–7 cm in *S. davisense*) and larger flowers (2–2.5 cm in diameter in *S. cordicitum* versus 1.3–2 cm in *S. davisense*). The prickles of *S. cordicitum* are more widely spaced (<20 per cm) than those of *S. citrullifolium* var. *setigerum* (>30 per cm). The flowers of *S. cordicitum* are generally smaller (2–2.5 cm in diameter) than those of *S. citrullifolium* var. *setigerum* (2.5–3.5 cm in diameter).

PARATYPES: UNITED STATES. Texas. Jeff Davis Co.: 30 mi W of Ft. Davis on US 166, 6000 ft, 17 Oct 1974 (fr), Heller 24 (UTEP); town of Valentine, Elder property, 30°35'40"N, 104°39'32"W, 1350 m, 7 Nov 2013 (fl, fr), J. Keeling 445 (MESA).

The three combinations below represent taxa previously recognized as varieties by Whalen (1979). These species each have distinctive morphological characteristics and geographical ranges that distinguish them from other species in sect. *Androceras*. Additionally, molecular phylogenetic analyses (Stern et al. 2010) have shown that they do not form monophyletic groups with the other varieties of their respective species.

Solanum knoblochii (Whalen) S. Stern, comb. & stat. nov. *Solanum citrullifolium* var. *knoblochii* Whalen, *Wrightia* 5:237. 1976. TYPE: MEXICO. CHIHUAHUA: Mojarachic, 16 Aug 1940, Knobloch 8006 (HOLOTYPE: US [00027510]).

Whalen (1976, 1979) designated the variety *S. citrullifolium* var. *knoblochii* and distinguished it from *S. citrullifolium* var. *setigerum* by the much denser pubescence of the latter (each cm of stem with over 25 prickles versus scattered prickles ≤ 20 per cm of stem in the former). It is also differentiated from *S. citrullifolium* var. *citrullifolium* by the short (≤ 1.2 mm), uniseriate hairs of the latter versus the presence of much longer (> 2 mm), uniseriate hairs in var. *knoblochii*. The easternmost distribution of var. *setigerum* overlaps with the westernmost distribution of var. *citrullifolium* in west Texas. However, *S. knoblochii* has a disjunct distribution from both of these varieties and is only known from two populations in the Tarahumara country of western Chihuahua, Mexico (Whalen 1976).

These distinct morphological characters, isolated geographical range, and evidence from molecular data (Stern et al. 2010) indicate that *S. citrullifolium* var. *knoblochii* should be recognized as a distinct species. The name *Solanum knoblochii* was retained, honoring Irving Knobloch, the first collector of this species in Chihuahua.

The remaining varieties of *S. citrullifolium*, vars. *citrullifolium* and *setigerum*, did not form a monophyletic group in Stern et al. (2010). Instead, they formed a strongly supported clade with *S. davisense* and *S. heterodoxum* var. *setigeroides*. These species have overlapping distributions and similar morphologies with the main difference being small flowers in *S. heterodoxum* var. *setigeroides* (corolla < 1.5 cm across, large anther < 5 mm), medium-sized flowers in *S. davisense* (corolla ca. 1.7 cm across, large anther 6–8 mm), and large flowers in both varieties of *S. citrullifolium* (corolla > 2 cm, large anther > 10 mm). There is also reported hybridization between *S. citrullifolium* var. *setigerum* and *S. heterodoxum* var. *setigeroides* (Whalen 1979). *Solanum heterodoxum* var. *setigeroides* is recognized as a distinct species below because it is not monophyletic with the other varieties of *S. heterodoxum* in the molecular phylogenetic analyses of Stern et al. (2010). Although *S. citrullifolium* vars. *citrullifolium* and *setigerum* also did not form a clade in Stern et al. (2010), resolution and support is low in this part of the tree. Further morphological and molecular data are needed to assess the taxonomic status of *S. citrullifolium* vars. *citrullifolium* and *setigerum* as well as that of *S. davisense*.

Conservation Status.—The status of *S. knoblochii* using the IUCN Red List Categories (IUCN 2010) is Data Deficient given the few collections and lack of long term monitoring. Recent collections, in addition to the original collections by Knobloch, show that the range of this species is approximately 34,000 km². This range is sufficient to place the species out of the Threatened category, but the limited number of collections (only five are known from two populations) is concerning and warrants Near Threatened status.

Two varieties of *S. heterodoxum* are designated as distinct species:

Solanum setigeroides (Whalen) S. Stern, comb. & stat. nov. *Solanum heterodoxum* var. *setigeroides* Whalen, *Wrightia* 5:237. 1976. TYPE: UNITED STATES. NEW MEXICO. Grant Co.: 12 mi W of Silver City, 4 Aug 1975, Whalen 201 (HOLOTYPE: LL [LL-00372877]); ISOTYPES: MO [MO-503667], WIS).

Solanum novomexicanum (Bartlett) S. Stern, comb. & stat. nov. *Solanum heterodoxum* var. *novomexicanum* Bartlett, Proc. Amer. Acad. Arts 44:628. 1909. *Androcera novomexicana* (Bartlett) Woot. & Standl., Contr. U.S. Natl. Herb. 16:170. 1913. TYPE: UNITED STATES. NEW MEXICO: Santa Fe, creek valley, foot of mountains, sunny side, 1847, *Fendler 673* (HOLOTYPE: GH [GH-00077421]; ISOTYPES: F, GH [GH-00077422], MO [MO-503664]).

Solanum heterodoxum var. *setigeroides* was recognized as distinct from *S. heterodoxum* vars. *heterodoxum* and *novomexicanum* due to the dense, narrow prickles on its stems (≥ 30 prickles per cm, mostly less than 0.5 mm in diameter versus ≤ 20 prickles per cm, often to 1 mm wide in the latter varieties). *Solanum heterodoxum* var. *novomexicanum* was differentiated from var. *heterodoxum* by its pentagonal-stellate corolla with narrow deltoid lobes versus pentagonal corollas with ample interpetalar tissue in the latter. The distributions of these varieties are also disjunct, with var. *heterodoxum* occurring in central Mexico from Veracruz to San Luis Potosí, var. *setigeroides* in northern Chihuahua, Mexico and westernmost Texas to central Arizona and New Mexico, and var. *novomexicanum* in northern New Mexico. Additionally, molecular phylogenetic data in Stern et al. (2010) found that these varieties do not form a monophyletic group and belong in distinct clades.

Etymology.—The name *S. setigeroides* was retained from the Latin word “setiger,” meaning “bristly,” referring to the bristly prickles of the stem. *Solanum novomexicanum* was originally recognized at the species level as *Androcera novomexicanum*, so the epithet was transferred and refers to fact that this species is endemic to New Mexico.

Conservation Status.—The conservation status of *S. setigeroides* according to the IUCN Red List Categories (IUCN 2010) is Least Concern. This is a widespread, weedy species with no obvious threats. Although *S. novomexicanum* is not as widespread or as frequently collected as *S. setigeroides*, its designation according to the IUCN Red List Categories (IUCN 2010) is also Least Concern due to its relatively weedy nature. Additionally, *S. novomexicanum* is afforded some protection with populations in Pecos Ruin National Historic Park and the Cibola National Forest.

KEY TO THE SPECIES OF SOLANUM SECTION ANDROCERAS
(REVISED FROM WHALEN 1979)

1. Cauline hairs stellate or multiangulate; corollas mostly yellow, rarely pale blue or white. _____ **S. tribulosum** S. Schauer
2. Corollas pale blue or white _____
2. Corollas yellow.
 3. Plants perennial, woody-based; cauline stellae echinoid, some of them with 15 or more rays; distribution in eastern Durango, Mexico _____ **S. johnstonii** Whalen
 3. Plants annual, taprooted; cauline stellae usually with 12 or fewer rays.
 4. Large anther essentially glabrous.
 5. Hilum of seed sunken in a deep notch; large anther hardly distinct, less than 6 mm long; corollas less than 2 cm across; cauline prickles broad-based, flattened and often recurved _____ **S. fructo-tecto** Cav.
 5. Hilum of seed not sunken in a deep notch; large anther very distinct from shorter ones, over 9 mm long; corollas more than 2 cm across; cauline prickles seldom much flattened or recurved _____ **S. rostratum** Dunal
 4. Large anther bearded on the proximal portion of the ventral surface _____ **S. angustifolium** Mill.
1. Cauline hairs simple, often glandular, occasionally absent; corollas usually violet, blue, or white, seldom yellow.
 6. Corollas violet or blue.
 7. Large anther 6 mm long or more; corollas 1.4 cm or more across; stigma unexpanded or only weakly capitate
 8. Plants perennial, woody- or corky-based; seeds plump, 2.8 mm long or more _____ **S. tenuipes** Bartlett
 8. Plants annual, taprooted; seeds lenticular, shorter than 3 mm
 9. Large anther 6–8 mm long; corollas ca. 1.7 cm across; buds obovoid, more or less radially symmetrical; large leaves often thrice pinnatifid, with acute ultimate lobes _____ **S. davisense** Whalen
 9. Large anther 10 mm long or more; corollas 2 cm or more across; buds noticeably curved, bilaterally symmetrical; large leaves usually only twice pinnatifid, with obtuse to acute ultimate lobes.
 10. Cauline hairs mostly <0.3 mm with occasional hairs reaching to 1 mm; distributed from central to west Texas to western Coahuila and eastern Chihuahua, Mexico _____ **S. citrullifolium** A. Braun
 10. Cauline hairs often reaching 2.5 mm in length; known only from western Chihuahua, Mexico _____ **S. knoblochii** (Whalen) S. Stern
 7. Large anther 5 mm long or less; corollas 1.5 cm or less across; stigma capitate, twice as thick as the style.
 11. Stems sparsely pubescent with simple, glandular hairs ca. 0.2 mm long; stems densely prickly, each cm with 30 or more acicular prickles, the bases less than 0.5 mm in diameter _____ **S. setigeroides** (Whalen) S. Stern
 11. Stems densely pubescent with simple, glandular hairs 0.2–0.4 mm long; stems sparsely prickly, each cm with 20 or fewer acicular prickles, the base up to 1 mm in diameter.

12. Corolla pentagonal, with ample, plicate interpetalar tissue; distribution in Mexico, from Veracruz to San Luis Potosí _____ **S. heterodoxum** Dunal
12. Corolla pentagonal-stellate, with narrowly deltoid lobes; distribution in U.S.A. (northern New Mexico) _____ **S. novomexicanum** (Bartlett) S. Stern
6. Corollas white or yellow.
13. Stems with well-spaced, acicular prickles; corollas pentagonal-stellate with ample, plicate interpetalar tissue, 2 cm or more across; seeds reticulately ridged.
14. Corolla yellow, 2.5 cm or more across; large anther bearded on the proximal portion of the ventral surface; distribution from tropical Mexico east to Honduras _____ **S. angustifolium** Mill.
14. Corolla white, 2–2.5 cm across; large anther glabrous; distribution in western Texas, USA _____ **S. cordicium** S. Stern
13. Stems with dense, filiform, bristle-like prickles; corollas distinctly stellate with little interpetalar tissue, 2.5 cm or less across; seeds radially ridged at margin.
15. Anthers of three sizes, the longest one flanked by two of intermediate length; mature seeds large, 3 mm or longer, with the hilum sunken in a deep notch; distribution from southern Arizona, USA to northern Sinaloa, Mexico _____ **S. lumholtzianum** Bartlett
15. Stamens dimorphic, one large, the other four smaller and essentially equal; mature seeds small, 3 mm long or less, not deeply notched; distribution from southern Sonora to Puebla and Guerrero, Mexico.
16. Leaves with simple and/or glandular hairs above, or glabrous; plants widespread along the Pacific slope of Mexico _____ **S. grayi** Rose
16. Leaves with stellate hairs above; endemic near Matamoros, Puebla, Mexico _____ **S. leucandrum** Whalen

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REFERENCES

- BOHS, L. 2005. Major clades in *Solanum* based on *ndhF* sequence data. In: R.C. Keating, V.C. Hollowell, and T.B. Croat, eds. A festschrift for William G. D'Arcy: The legacy of a taxonomist. *Mongr. Syst. Bot. Missouri Bot. Gard.* Vol. 104. Missouri Botanical Press, St. Louis, Missouri, U.S.A. Pp. 27–49.
- IUCN STANDARDS AND PETITIONS SUBCOMMITTEE. 2010. Guidelines for using the IUCN Red List Categories and Criteria. Version 8.0. Prepared by the Standards and Petitions Subcommittee in March 2010. Downloadable from <http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf>. [accessed 5 October 2010].
- KNAPP, S., L. BOHS, M. NEE, & D.M. SPOONER. 2004. Solanaceae – a model for linking genomics with biodiversity. *Comp. Funct. Genomics* 5:285–291.
- LEVIN, R.A., N.R. MYERS, & L. BOHS. 2006. Phylogenetic relationships among the “spiny solanums” (*Solanum* subgenus *Leptostemonum*, Solanaceae). *Amer. J. Bot.* 93:157–169.
- STERN, S.R., T. WEESE, & L. BOHS. 2010. Phylogenetic relationships in *Solanum* section *Androceras* (Solanaceae). *Syst. Bot.* 34:885–893.
- STERN, S.R., M.F. AGRA, & L. BOHS. 2011. Molecular delimitation of clades within New World species of the “spiny solanums” (*Solanum* subg. *Leptostemonum*). *Taxon* 60:1429–1441.
- WEESE, T.L. & L. BOHS. 2007. A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Syst. Bot.* 32:445–463.
- WHALEN, M.D. 1976. New taxa of *Solanum* sect. *Androceras*. *Wrightia* 5:228–239.
- WHALEN, M.D. 1979. Taxonomy of *Solanum* section *Androceras*. *Gentes Herb.* 11:359–426.